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ECOSYSTEMS

Abundance and Impact on Soil Properties of Cathedral and Lenticular Termite Mounds in Southern Indian Woodlands

Pascal Jouquet,[1,2]* Etienne Airola,[1,2] Nabila Guilleux,[1,2] Ajay Harit,[2]
Ekta Chaudhary,[2,3] Séraphine Grellier,[4] and Jean Riotte[2,5]

[1]Institute of Ecology and Environmental Sciences (UMR 242 iEES Paris, UPMC, CNRS, IRD, INRA, UPEC, Univ. P. Diderot), Institute of Research for Development (IRD), 32 av. H. Varagnat, 93143 Bondy, France; [2]Indo-French Cell for Water Science (IFCWS), Civil engineering Department, Indian Institute of Science, Bangalore, Karnataka 560 012, India; [3]Center for Ecological Studies (CES), Indian Institute of Science, Bangalore, Karnataka 560 012, India; [4]IPAPE, CITERES UMR 7324, Université François Rabelais, 35 allée Ferdinand de Lesseps, 37200 Tours, France; [5]GET-OMP, UMR 5563 CNRS/Univ. P. Sabatier/IRD, 14 avenue E. Belin, 31400 Toulouse, France

ABSTRACT

Despite the acknowledged roles of termites in tropical ecosystems, the majority of published studies of epigeal mounds still address the African fauna and are principally concerned with spatial patterns and putative inter-colony competition, rather than the links between parent soil properties and mound establishment. Further, information about the effects of habitat disturbance, and especially fragmentation, is lacking. This study assessed the abundance and distribution of the cathedral- and lenticular-type aboveground mounds of fungus-growing termites (Macrotermitinae), which are a common feature of South Indian woodlands, in relation to soil properties (vertisol vs. ferralsol) and habitat fragmentation (forest vs. highway margins). Mound abundance averaged 3.5 (standard error, SE 0.8) ha^{-1} (cathedral) and 12.9 (SE 2.1) ha^{-1} (lenticular), but was not influenced either by soil properties or disturbance. However, the volume of soil stored in the mounds varied between 27 (SE 8) $m^3\ ha^{-1}$ (ferralsol) and 47 (SE 6) $m^3\ ha^{-1}$ (vertisol). At the watershed scale, such volumes are equivalent to a 3.1-mm layer of soil if spread evenly across the landscape, roughly the same as the estimated erosion over the life of a typical mound. Significantly more nutrients were stored in lenticular mounds, especially on the vertisol, but the significance of these at the ecosystem level was considered small. In conclusion, this study suggests that termite mounds, and especially lenticular mounds, have a significant impact on soil dynamics at the watershed scale but a limited impact on the distribution of C and nutrients.

Key words: spatial distribution; termite mound; C and nutrient stocks; ferralsol; vertisol; habitat fragmentation; India.

INTRODUCTION

Fungus-growing termites (Isoptera, Macrotermitinae) are often regarded as soil engineers, and notably so in the drier tropical ecosystems in which they are common in Africa and Asia (La-

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**Corresponding author; e-mail:* pascal.jouquet@ird.fr

velle and others 1997; Jouquet and others 2011). This role is well established at the point scale, where tunneling, bioturbation, and litter consumption are obvious activities, but soil is also accumulated into conspicuous mounds. The mounds differ in physical, chemical, and biological properties from their parent soils (Abe and others 2011; Menichetti and others 2014; Seymour and others 2014; Erens and others 2015a), such that based on studies in African ecosystems it is assumed their contribution to soil dynamics, nutrient recycling vegetation growth and diversity, and herbivory patterns is significant (Traore and others 2008, 2015; Moe and others 2009; Sileshi and others 2010; Pringle and others 2010). However, clear evidence requires data at the landscape level, which are generally lacking.

At the broad scale, variations in rainfall and soil geology are key factors influencing termite mound distribution (Meyer and others 1999; Levick and others 2010; Davies and others 2014). At a more local scale, termite mound density is considered to be mostly regulated by biotic processes including the type of vegetation and the predation or competition pressures (Korb and Linsenmair 1998; Davies and others 2014). Although termite impacts on soils have been extensively documented, the influence of soil pedological properties on termite populations (Pequeno and others 2015) and termite mound distribution remains poorly known. However, recent studies show that soil pedological properties can influence the shape and properties of termite mounds at the scale of a few ha (Jouquet and others 2015, 2016), then possibly influencing their dynamics and distributions at the scale of the landscape. Moreover, the influence of habitat fragmentation resulting from human activities on termite mounds remains unknown, despite the fact that land-use intensification and habitat fragmentation are known to have a local impact on termite diversity and activity (Eggleton and others 1994, 1997; Black and Okwakol 1997; Crist 1998; Davies and others 2003; Dambros and others 2013). It can therefore be proposed that soil properties and disturbance are also likely to affect mound distribution significantly, with consequent effects on their role as temporary reservoirs of mineral and organic materials.

Termite mounds can have a great variety of shapes but, broadly speaking, fungus-growing termites typically build two types of mound. The first type corresponds to the mounds that are erected vertically by only one colony (for example, Collins 1979) and that can bear spectacular features such as turrets (for example, nests of *Macrotermes bellicosus*), chimneys (for example, *M. jeanneli*), or spires (for example *M. michaelseni*) (Josens and others 2016). The second type of termite mound are ‘‘hillocks’’ or ‘‘lenticular mounds’’ that are very variable in size and occupied by several species, especially fungus-growing termites (for example, *Odontotermes aff. pauperans*), as well as many other invertebrate and/or vertebrate taxons (Darlington 1985; Choosai and others 2009). The density, spatial distribution, and chemical properties of the first type of mound have been intensively studied in African savannah and gallery forests with the genus *Macrotermes* (for example, Korb and Linsenmair 2001a; Jouquet and others 2004; Mujinya and others 2014). However, much less information is available on the properties of lenticular mounds, although they are also commonly observed in African and Asian landscapes (Konaté and others 1999; Jouquet and others 2004; Choosai and others 2009; Miyagawa and others 2011; Erens and others 2015b; Josens and others 2016). In particular, the amount of carbon and nutrients temporarily stored within these two types of constructions has never been compared at the ecosystem scale and in considering the influence of the soil pedological properties. Information is therefore needed to better understand how these two types of mounds interact between them and with their environment, if they do, in order to increase our knowledge of how termites control the distribution of nutrients in ecosystems.

In southern India, these two types of termite mounds are commonly observed in woodlands. The first type of mound is built by only one fungus-growing termite species, *Odontotermes obesus*, whereas several species have been recorded in the second type of mound (for example, *Odontotermes brunneus, O. giriensis, O. gurdaspurensis, O. microdentatus, O. redamanni, O. obesus,* and *Ceylonitermes indicola)* (Chhotani and Bose 1979). This study examines how the two mound types are accommodated in relation to soil and disturbance, and whether termites control the distribution of nutrients in ecosystems. Our hypotheses were that the different termite colonies observed in these two types of mound are likely to compete for resources because they occupy the same trophic niche (feeding on decaying wood and leaf litter, usually foraged from the surface of the ground) and that the spatial distribution and physico-chemical properties of their mounds are also likely to be influenced by soil properties and habitat fragmentation.

MATERIALS AND METHODS

Study Site

This study was carried out in the Mule Hole watershed (4.3 km^2) in the Bandipur Tiger Reserve located in the Chamarajanagar districts of Karnataka state in southern India (11°44′N, 76°27′E). This sub-humid tropical forest is characterized by alternating dry and rainy seasons (mean annual temperature ~27°C, and total annual rainfall from 1000 to 1500 mm on average, with an average over the last thirty years of 1100 mm y^{-1}) (Braun and others 2009; Riotte and others 2014). A main road and several paths cross the forest with highway margins fragmenting the habitat approximately 20–25 m on each side of the road. In this environment, the forest has a more open canopy, and the development of herbaceous plants and shrubs is limited by annual cutting and fire. Soils are mainly ferralsol (80% of soils), dominated by kaolinite (1:1 clay), and characterized by an accumulation of iron and aluminum, and vertisol (20%), dominated by smectite (2:1 clay) (Barbiero and others 2007). The plant cover is a dry deciduous forest characterized mainly by ''ATT'' facies (*Anogeissus latifolia*, *Tectona grandis*, and *Terminalia crenulata)*, and the grass cover is dominated by *Themeda triandra* (elephant grass). The watershed is also affected by two invasive weed species, *Lantana camara* and *Chromolaena odorata*, native of tropical America and introduced as garden ornaments (Riotte and others 2014).

Data Collection

Two types of termite mounds were observed in the Mule Hole watershed (Figure 1). The first type is the cathedral-shaped termite mound built by *Odontotermes obesus*, which are very similar in shape to those built by *Macrotermes bellicosus* in Africa, whereas the second is a lenticular-shaped termite mound. Termite mound distribution was studied in the two dominant soil type environments, namely the ferralsol and vertisol areas, and two different habitat types: inside the forest or in the highway margin ($n = 3$ in each case, average size of the plot = 2.1 ha, SE 0.4). Data were collected during the dry season from March to May 2015. In total, 579 termite mounds were identified (432 lenticular and 147 cathedral). Cathedral mounds were recorded as living (that is, containing active colonies) or abandoned, when the center of a nest was broken. All the lenticular mounds were considered in

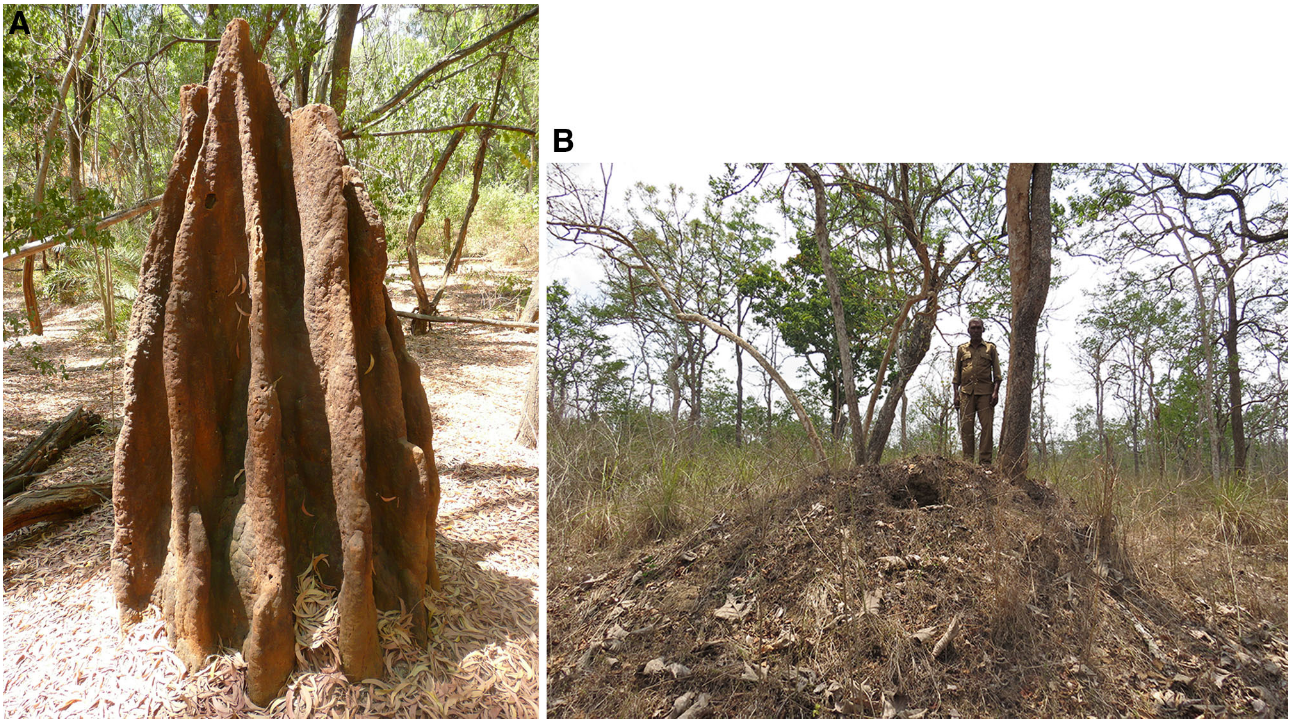

Figure 1. Examples of cathedral (**A**) and lenticular (**B**) mounds. Cathedral mounds are edified by *Odontotermes obesus*, whereas the origin and dynamics of lenticular mounds remain unknown. Lenticular mounds can be occupied by several termite species, including *Odontotermes brunneus*, *O. giriensis*, *O. gurdaspurensis*, *O. microdentatus*, *O. redamanni*, *O. obesus*, and *Ceylonitermes indicola*. Photos P. Jouquet 2016.

this study because their status as dead or alive was impossible to estimate in the field (a hole in the mound does not necessarily mean that all the termite colonies were killed).

Data Analysis

In each plot, the GPS coordinates of termite mounds were recorded. The density of living termite mounds (number ha^{-1}) was analyzed for the two termite mound categories (cathedral vs. lenticular) in each plot.

The surface on the ground and the volume of soil used by termites to produce cathedral mounds were assessed by measuring the height and diameter of termite mounds in the field and comparing them as cones with the following formula: $V_c = (\pi \times R^2 \times h)/3$, where R is the average radius of the mound at its base and h its height. The same approach was used for lenticular mounds but considering mounds as domes and using the following formula: $V_d = (\pi \times h \times (3R^2 + h^2))/6$. The erosion of cathedral mounds can lead to the accumulation of soil at their base. This volume of soil was assumed to be dome-shaped and its volume was calculated as for V_d (see Jouquet and others 2016 for more information).

Undisturbed soil samples were collected using 250 cm^3 cores to determine soil bulk density at 0–10 cm deep in the control environments without visible termite activity (distance to termite mound ≥5 m) and in lenticular mounds. Bulk densities of cathedral soils were determined with the paraffin method (Pansu and others1998). Soil organic matter (SOM) was assessed from C and N concentrations using an elemental analyzer Flash 2000 HT. The exchangeable cation contents (Ca, Mg, Na, K, Fe, Mn, and Al) were measured at soil pH and extraction with cobalthyhexamine (AFNOR, NF ISO 23470). Soil physical and chemical properties were carried out with $n = 3$ replicates per treatment. The nutrient content (C, N, and exchangeable cations) was assessed by multiplying the average termite mound density (in ha^{-1}) by the average termite mound volume (in m^3 $mound^{-1}$), the soil density (in g cm^{-3}), and nutrient concentration (in g g^{-1} soil). The ratio of the stock of chemical nutrients stored in termite mounds to the stock of nutrients contained in 0–10 cm soil surface layer (in %) was thereafter calculated.

Statistical Analyses

Relationships between cathedral and lenticular mound densities in the 12 different plots were tested using linear regression. The spatial distributions of living termite mounds and their interactions were analyzed using the Diggle's nearest neighbor function *G(w)* and Ripley's *K(d)* function (Ripley 1981; Diggle 1983). *G* and *K* functions analyzed the spatial patterns of termite mounds (lenticular and living cathedral mounds alone or together: ALL) and their interactions (Barot and others 1999; Jouquet and others 2004). Observed functions for the measured samples were compared to the theoretical functions under the null hypothesis H_0 of a complete spatial randomness (or independence in the spatial association test) after 999 Monte Carlo test simulations. Using this method, we could test whether (i) the distribution of the observed samples is regular, random, or clustered and (ii) the relationships between two types of sample points are positive (association), negative (repulsion), or neutral (independence).

Differences in mound density, termite mound soil volume, and soil physical and chemical properties were analyzed using analysis of variance (ANOVA) with soil, habitat, and termite mound type as independent variables, after verification of residual normality using the Shapiro–Wilk test and homogeneity of variances. When residues were not normally distributed, variables were log transformed. Differences between means were then assessed with Tukey's test.

Data were analyzed with QGis 2.6.1 and R 3.1.2 with the ''spatstat'' package (Baddeley and others 2015). All tests were performed at the $P < 0.05$ significance level.

RESULTS

Termite Mound Density and Distribution

Cathedral and lenticular mound densities were not influenced by the soil type but a significant interaction was observed between the termite mound type and the habitat (Table 1). Figure 2 shows that in both habitats (forest vs. highway margin) lenticular mounds were significantly more abundant than cathedral, with 12.89 mound ha^{-1} in average (standard error, SE 2.06) and 3.48 mound ha^{-1} (SE 0.79), respectively ($P < 0.05$).

Termite mound (cathedral + lenticular) distributions were variable and site-specific (Table 2). *G(w)* and *K(d)* functions provided the same results, with two exceptions. *G(w)* identified the regular pattern of termite mounds in For2 in the vertisol and the clustered pattern of lenticular mounds in Rd2 in the ferralsol, whereas *K(d)* did not. Half of the plots were characterized by a random distribution of termite mounds, irrespective of the soil

Table 1. Results of the Three-Way ANOVA Testing the Influence of Termites (Cathedral vs. Lenticular), Soil Type (Ferralsol vs. Vertisol), and Habitat (Forest vs. Highway Margin) on Termite Mound Density

	$F_{1,16}$	*P*
Termite (1)	32.06	<0.001***
Soil (2)	0.80	0.383
Habitat (3)	12.36	0.002**
(1) × (2)	1.39	0.255
(1) × (3)	5.66	0.030*
(2) × (3)	1.83	0.194
(1) × (2) × (3)	0.87	0.365

*Probabilities at P = 0.05, n = 3. *** <0.001, ** <0.01, * <0.05.*

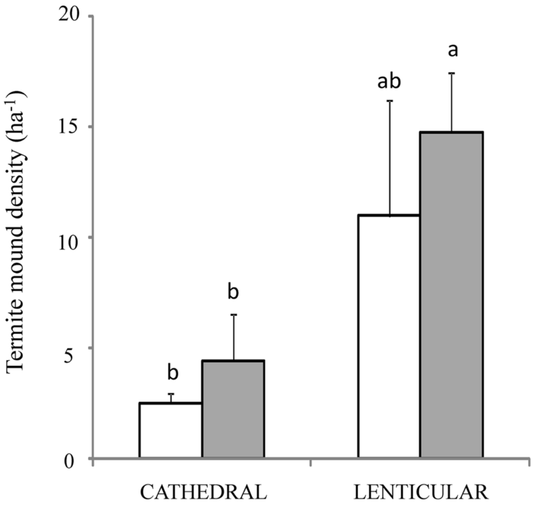

Figure 2. Cathedral and lenticular mound densities (in number ha^{-1}) in the highway margin (in *white*) and inside the forest (in *black*). Histograms with the *same letters* are not significantly different at *P* = 0.05. *Bars* represent standard errors, *n* = 6.

type (three plots in both the ferralsol and the vertisol). The termite mound distribution was clustered in three plots in the ferralsol (For2, Rd1, Rd3) and in two plots in the vertisol area (For3 and Rd2), and displayed a regular pattern in only one plot (For2 in vertisol). Cathedral mounds were almost always randomly distributed, except in three plots. Any non-random patterns found were therefore mainly explained by the distribution of lenticular mounds (six plots).

No significant relationship was found between lenticular and cathedral mound densities ($y = 0.167x + 1.32$, $n = 12$, $R^2 = 0.19$, $P = 0.158$, data not shown). In addition, the *G(w)* and *K(d)* functions suggested spatial independence between these two mound types ($P > 0.05$) in most cases (Table 3). Significant interactions were only measured in two plots in the ferralsol area where association and repulsion patterns were measured with the *K(d)* function in For2 and Rd2, respectively, and only one plot in the vertisol area where *G(w)* showed an association between the two mound types in Rd2.

Importance of Termite Mounds at the Ecosystem Scale

Significantly different volumes and surfaces occupied by cathedral and lenticular mounds were found in the ferralsol and vertisol ($P < 0.05$, Table 4). However, these variables were not influenced by the habitat type (forest vs. highway margin, $P > 0.05$). Figures 3A, B shows that the volume and surface occupied by cathedral mounds were similar in ferralsol and vertisol ($P > 0.05$ between both). In contrast, significant differences were measured for lenticular mounds with higher values in vertisol than ferralsol areas. Figure 3A shows that the surface occupied by cathedral mounds was much lower than the surface observed for lenticular mounds (2.98 m^2 vs. 15.99 and 32.83 m^2, for cathedral and lenticular in ferralsol and vertisol, respectively). Similarly, lower soil volumes were used in cathedral mounds than lenticular mounds with 3.47 vs. 23.88 and 43.39 m^3, for cathedral and lenticular in ferralsol and vertisol, respectively (Figure 3B).

The C stocks and nutrients temporarily stored in termite mounds were low at the ecosystem scale in ferralsol with values below 3% of that measured in the 0–10 cm soil surface layer (Table 5). In vertisol, the termite mounds contained significantly more C and other nutrients than in ferralsol ($P < 0.05$ for all elements) with values ranging from about 4 to 13%. However, the distinction between cathedral and lenticular shows that most of the elements were stored within lenticular mounds in both soil types, with the exception of Mn ($P > 0.05$ between both).

DISCUSSION

Spatial Distribution of Termite Mounds

Because termites are sensitive to habitat disturbance (Basu and others 1996; Gathorne-Hardy and others 2002; Roisin and Leponce 2004), they have been described as bio-indicators of habitat change in the tropics (Dosso and others 2012) and as very suitable groups for illustrating the effects of ecosystem fragmentation (Desouza and Brown

Table 2. Spatial Distribution Analysis of Living Termite Mounds (Cathedral, Lenticular, or Both Together: ALL) Using *G(w)* and *K(d)* Tests of Spatial Distribution

	All		Cathedral		Lenticular	
Plot	*G(w)*	*K(d)*	*G(d)*	*K(d)*	*G(w)*	*K(d)*
Ferralsol						
For1	0.158 H_0	0.054 H_0	0.116 H_0	0.109 H_0	0.901 H_0	0.512 H_0
For2	**0.001 Cluster**	**0.001 Cluster**	**0.002 Cluster**	NA	**0.002 Cluster**	**0.001 Cluster**
For3	0.654 H_0	0.819 H_0	0.949 H_0	NA	0.634 H_0	0.398 H_0
Rd1	**0.017 Cluster**	**0.038 Cluster**	0.260 H_0	NA	**0.040 Cluster**	**0.030 Cluster**
Rd2	0.398 H_0	0.294 H_0	0.984 H_0	NA	0.828 H_0	0.744 H_0
Rd3	**0.002 Cluster**	**0.004 Cluster**	**0.001 Cluster**	**0.007 Cluster**	**0.043 Cluster**	0.067 H_0
Vertisol						
For1	0.791 H_0	0.804 H_0	0.776 H_0	NA	0.969 H_0	0.952 H_0
For2	**0.032 Regular**	0.222 H_0	NA	NA	**0.025 Regular**	0.176 H_0
For3	**0.002 Cluster**	**0.001 Cluster**	**0.029 Cluster**	**0.030 Cluster**	**0.026 Cluster**	**0.001 Cluster**
Rd1	0.119 H_0	0.069 H_0	0.127 H_0	NA	0.09 H_0	0.109 H_0
Rd2	**0.001 Cluster**	NA	0.170 H_0	NA	**0.036 Cluster**	NA
Rd3	0.711 H_0	0.368 H_0	0.541 H_0	NA	0.509 H_0	0.274 H_0

The P values indicate the probability of accepting H_0 for spatial randomness. Significant results are highlighted in bold characters. The treatments were soil (ferralsol or vertisol) and habitat types (forest 'For' or highway margin 'Rd') (n = 3 plots per treatment). Patterns are random (H_0), clustered, or regular. NA for non-applicable when sample numbers per plot were too low to calculate K(d).

Table 3. Spatial Interactions Between Living Termite Mounds (Cathedral and Lenticular) in the Forest (''For'') or in the Highway Margin (''Rd'') Using *G(w)* and *K(d)* Tests of Spatial Distribution

	Cathedral to lenticular		Lenticular to cathedral	
Plot	*G(w)*	*K(d)*	*G(w)*	*K(d)*
Ferralsol				
For 1	0.511 H_0	0.260 H_0	0.287 H_0	0.193 H_0
For 2	0.539 H_0	**0.006 Association**	0.422 H_0	**0.018 Association**
For 3	0.741 H_0	0.426 H_0	0.479 H_0	0.521 H_0
Rd 1	0.840 H_0	0.482 H_0	0.192 H_0	0.932 H_0
Rd 2	0.777 H_0	**0.025 Repulsion**	0.991 H_0	**0.029 Repulsion**
Rd 3	0.258 H_0	0.279 H_0	0.281 H_0	0.736 H_0
Vertisol				
For 1	0.479 H_0	0.845 H_0	0.076 H_0	0.951 H_0
For 2	0.196 H_0	0.906 H_0	0.082 H_0	0.957 H_0
For 3	0.499 H_0	0.852 H_0	0.091 H_0	0.946 H_0
Rd 1	0.969 H_0	0.412 H_0	0.298 H_0	0.401 H_0
Rd 2	0.847 H_0	0.775 H_0	**0.019 Association**	0.981 H_0
Rd 3	0.463 H_0	0.341 H_0	0.320 H_0	0.062 H_0

Probabilities are testing the null hypothesis H_0 of pattern independence between termite mounds. Significant results are highlighted in bold characters. NA for non-applicable when the sample number was too low. Interactions are independence (H_0), association, or repulsion.

Table 4. Results of the Three-way ANOVA Testing the Influence of Termites (Cathedral vs. Lenticular), Soil Type (Ferralsol vs. Vertisol), and Habitat (Forest vs. Highway Margin) on the Surface and Volume of Termite Mounds

	Surface		Volume	
	$F_{1,16}$	P	$F_{1,16}$	P
Termite (1)	68.42	<0.001 ***	60.31	<0.001 ***
Soil (2)	9.92	0.006 **	5.80	0.028 *
Habitat (3)	1.27	0.276	1.00	0.332
(1) x (2)	0.56	0.464	1.13	0.303
(1) x (3)	3.95	0.064	2.98	0.104
(2) x (3)	0.21	0.650	0.21	0.653
(1) x (2) x (3)	0.76	0.397	1.83	0.195

*Probabilities at P = 0.05 are shown. *** <0.001, ** <0.01, * <0.05.*

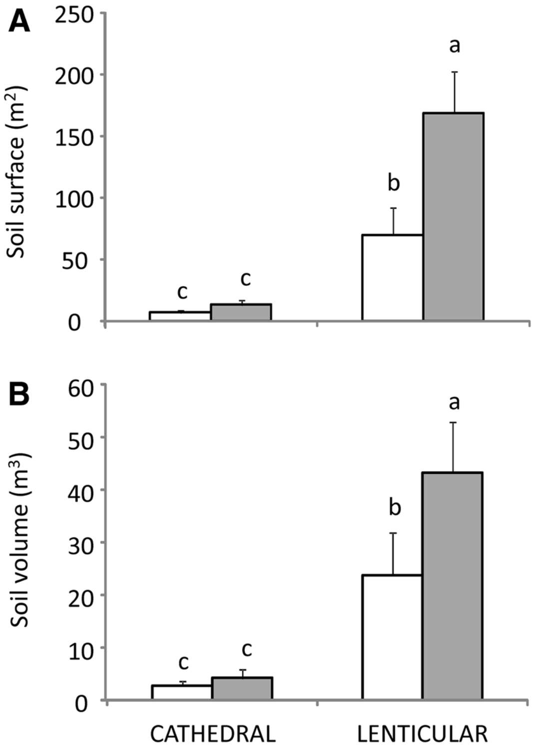

Figure 3. Surface area (**A**) and volume (**B**) of cathedral and lenticular mounds (in m^2 ha^{-1} or m^3 ha^{-1}) in the ferralsol (in *white*) and vertisol (in *gray*). Histograms with the *same letters* are not significantly different at $P = 0.05$. *Bars* represent standard errors, $n = 6$.

1994). In addition, studies carried out in Africa with *Macrotermes* sp. showed that termite mounds are also relevant indicators of the soil conditions and hydrology (Pomeroy 1977; Meyer and others 1999; Attignon and others 2005; Levick and others 2010; Arveti and others 2012). For example, too much clay prevents *Macrotermes* sp. mound establishment because of low permeability and increased periods of inundation, and too little clay is likely to prevent or limit mound construction (Levick and others 2010). In our study, neither the soil (vertisol vs. ferralsol) nor habitat type (forest vs. highway margin) influenced cathedral and lenticular mound densities, thus suggesting a limited effect of the environment on termite mound density. These results are in agreement with the fact that *O. obesus* only slightly and passively increase the clay content in mounds and that this effect is similar for all soil types (Jouquet and others 2016). Therefore, we assume that the termite species building cathedral and lenticular mounds are less dependent on the soil properties, including clay content and mineralogy, than *Macrotermes* sp. in Africa.

At our study site, cathedral mound abundance reached about 3.5 mound ha^{-1}. This value is similar to that measured for *Macrotermes* sp. in Africa (for example, values ranging from <1 to 7 mounds ha^{-1} have been recorded by Pomeroy 1977; Collins 1981; Lepage 1984; Meyer and others 1999; Levick and others 2010; Davies and others 2014), although *Macrotermes* sp. mound densities can also reach very high values in some circumstances (for example, >30–100 mounds ha^{-1} have been recorded by Lepage 1974 and Korb and Linsenmair 2001a in West Africa). On the other hand, lenticular mound abundance reached approximately 13 mounds ha^{-1} (3.5-fold more than cathedral mounds). Moreover, most of the soil processed by termites was stored in lenticular mounds (87% in ferralsol and 93% in vertisol), although this may not necessarily represent the amount of soil that is annually bioturbated for producing termite sheeting, subterranean galleries, and fungus-comb chambers (Abbadie and Lepage 1989; Jouquet and

Table 5. Ratio of the Stock of Chemical Nutrients (Total C and N, and Exchangeable Cations: Ca, Mg, Na, K, Fe, Mn, and Al) Contained in Cathedral and Lenticular Mounds to the Stock of Nutrients Contained in 0–10 cm Soil Surface Layer in the Ferralsol and Vertisol (in % per ha)

	C	N	Ca	Mg	Na	K	Fe	Mn	Al
Ferralsol									
Cathedral	0.14^{C}	0.13^{C}	0.19^{C}	0.23^{C}	0.41^{D}	0.20^{C}	0.34^{C}	1.21^{A}	0.31^{B}
	(0.02)	(0.02)	(0.01)	(0.01)	(0.02)	(0.03)	(0.03)	(0.21)	(0.03)
Lenticular	1.61^{B}	1.82^{B}	2.47^{B}	1.74^{B}	2.66^{B}	2.63^{B}	1.91^{B}	1.37^{A}	1.59^{A}
	(0.18)	(0.17)	(0.14)	(0.38)	(0.28)	(0.72)	(0.24)	(0.04)	(0.21)
Vertisol									
Cathedral	0.46^{C}	0.41^{C}	0.84^{C}	1.54^{B}	1.74^{C}	0.42^{C}	0.87^{BC}	2.51^{A}	0.38^{B}
	(0.03)	(0.05)	(0.05)	(0.21)	(0.23)	(0.02)	(0.33)	(0.47)	(0.15)
Lenticular	3.69^{A}	3.82^{A}	7.96^{A}	11.94^{A}	4.50^{A}	6.91^{A}	9.27^{A}	1.50^{A}	3.96^{A}
	(0.35)	(0.44)	(0.48)	(1.52)	(0.38)	(1.89)	(3.53)	(0.71)	(1.67)
Total:									
Cathedral + Lenticular									
Ferralsol	1.76^{B}	1.96^{B}	2.66^{B}	1.97^{B}	3.07^{B}	2.83^{B}	2.25^{B}	2.58^{B}	1.90^{B}
	(0.19)	(0.18)	(0.14)	(0.39)	(0.29)	(0.73)	(0.25)	(0.18)	(0.19)
Vertisol	4.15^{A}	4.23^{A}	8.79^{A}	13.47^{A}	6.23^{A}	7.33^{A}	10.14^{A}	4.02^{A}	4.34^{A}
	(0.37)	(0.48)	(0.45)	(1.34)	(0.16)	(1.91)	(3.83)	(0.53)	(1.81)

Values in parentheses are standard errors, values with the same letter are similar at $P = 0.005$, $n = 3$.

others 2003) or that processed by incipient belowground colonies. Consequently, although most of the studies focused on cathedral mounds, our study shows that they may only represent the ‘tip of the iceberg’ and that termite bioturbation activity can be significantly underestimated if lenticular mounds are not considered.

In other studies, termite mound distribution was also found to be random (Korb and Linsenmair 2001a, 2001b; Mujinya and others 2014), to aggregate (Pomeroy 1977; Schuurman and Dangerfield 1997; Korb and Linsenmair 2001a, 2001b; Grohmann and others 2010), or to show a regular pattern (Collins 1981; Korb and Linsenmair 2001a; Pringle and others 2010; Davies and others 2014). At the broad scale, variations in rainfall and soil geology are key factors influencing termite mound distribution (Meyer and others 1999; Levick and others 2010; Davies and others 2014). At a more local scale, the presence of predators and competitors (intra- and inter-specific interactions) are usually considered to be of primary importance in the regulation of termite mound distribution (Collins 1981; Lepage 1984; Crist 1998; Korb and Linsenmair 2001b; Grohmann and others 2010). However, less is known about how termite mound pattern locally varies with soil properties and habitat fragmentation. In our study, half of the plots were randomly distributed, irrespectively of soil properties and habitat types. The spatial pattern of the termite mounds could not be explained by the interactions between the two mound types, except in three plots. The hypothesis that the two mound types are spatially independent was also strengthened by the absence of a relationship between cathedral and lenticular mound densities. Consequently, the assumptions that soil type, habitat fragmentation, and/or inter-specific competition between termite colonies are having an effect on the spatial pattern of termite mounds could be rejected. This conclusion has, however, to be considered with caution because incipient belowground colonies were not considered in this study, and it is likely that competition between them and those of mounds occurs. The spatial pattern of termite mounds was site-specific in our study site, and thus we suggest that it mostly results from the influence of predators that are also spatially and temporarily heterogeneously distributed in the ecosystem. Amongst the wild animals that are able to cause major damage to termite nests, ants and sloth bears (*Melursus ursinus*) are probably the most common in our study site. The impact of ants has never been studied in our study site but predation by sloth bears has been recorded. The diet of sloth bear is largely based on fruits and insects and termites can constitute a significant proportion (up to 81%), especially during the wetter months (Ramesh and others 2012). Pangolins, wild pigs, elephants, and monkeys are also very active in the Tiger reserve. It is likely that they also contribute to termite mound degradation, either to feed on termites (pangolins and wild pigs) or to consume termite mound soils, as observed in Africa with elephants and monkeys (Aufreiter and others 2001; Holdo and McDowell 2004; Reynolds and others 2015), although these behaviors have not been evidenced in Asia.

Impact of Termite Mounds on Soil Dynamics and Nutrient Distribution

Few studies have focused on the distribution of termite mounds in ecosystems and quantified the amount of nutrients that are temporarily stored within them at the ecosystem scale. Despite similar abundance in the two soil types, lenticular mounds represented a higher surface and volume of soil in vertisol than in ferralsol. This confirms that although soil type did not influence termite mound density, termite mound properties depend to a large extent on the soil properties in their environment (Jouquet and others 2016).

In total, we estimated that the volume of soil currently stored in termite mounds (cathedral plus lenticular mounds) reaches 27 m^3 ha^{-1} in ferralsol and 47 m^3 ha^{-1} in vertisol. At the watershed scale, these amounts would be equivalent to a soil layer of 3.1 mm soil ha^{-1}, or 2.7 and 4.7 mm ha^{-1} in ferralsol (80% of the watershed) and vertisol (20%), respectively. These values can be compared to the processes controlling soil dynamics (that is, saprolite production and soil erosion rates) with simple assumptions on termite mound turnover. Using the sodium fluxes exported from the Mule Hole watershed during the last decades, Braun and others (2009) and Riotte and others (2014) estimated that the present-day saprolite production rate ranges from 22 to 30 mm Ky^{-1}. Current erosion rates, estimated from monitoring suspended matter in the stream for the last decade, is similar to the saprolite production rate which indicates that present-day pedogenesis is at equilibrium. The turnover rate of termite mound soil is actually less constrained than the soil production rate. Recent dating of very large termite mounds (3.5 to >6 m height, 5 m on average) in Africa found ages up to 2200 years old (Erens and others 2015b). In these conditions, mound turnover rates should reasonably range from 100 years to—as an extreme—1000 years (Darlington 1985), which corresponds to a soil turnover of 3.1–31 mm ky^{-1}, that is, equivalent to the range of denudation rates. Our results therefore suggest an important impact of termite activity on soil dynamics at the watershed scale. They also highlight the need for a better understanding of the lifetime of termite mounds, their evolution in size, degradation once the colonies are dead, and how this soil returns to the environment.

As a consequence of the higher volume of lenticular mounds in vertisol than in ferralsol, we found that significantly more nutrients were contained in vertisol than in ferralsol. In addition, the distinction between cathedral and lenticular shows that most of the elements were stored within lenticular mounds in both soil types. Termite mounds are usually locally considered as hotspots or patches of nutrients (for example, Salick and others 1983; Holdo and McDowell 2004; Bonachela and others 2015; Cramer and Midgley 2015). However, the C and nutrient storage in termite mound soils were low at the ecosystem scale compared to the 0–10 cm soil surface layer. Non-significant results were obtained in ferralsol (percentage of nutrients $<5\%$ in all cases). In vertisol, termite mounds occupy 0.36% of the surface ($\sim$36 m^2 ha^{-1}) but stored high levels of Ca, Mg, Na, K, and Fe (from 6 to 13%), whereas their influence on C, N, Mn, and Al was lower with values below 5%. Because plant productivity is mainly limited by N and P in tropical ecosystems (Koerselman and Meuleman 1996), this finding confirms the studies of Brossard and others (2007) who concluded that C and nutrient storage in mounds were insignificant for the vegetation in relation to the overall nutrient capital in the top 15 cm of soil.

CONCLUSIONS

In conclusion, this study highlighted that lenticular mounds have a stronger impact on soil and nutrient dynamics than cathedral mounds. Although conspicuous features of many tropical ecosystems, cathedral mounds appear to only play limited roles at the ecosystem scale and further studies are needed to determine if this observation is also valid in other contexts, such as in African savannahs where lenticular mounds are also commonly observed (Darlington 1985; Konaté and others 1999; Jouquet and others 2004; Josens and others 2016). Most termite-mediated soil bioturbation is channeled through the construction of lenticular mounds, which potentially explains soil erosion at the ecosystem scale. The influence of termite mounds on the distribution of soil nutrients was rather limited and only concerned Mg, Ca, K, Na, and Fe, which are less important elements than N and P in tropical ecosystems. This study also confirms the findings of other studies showing in African savannas that the influence of termite mounds on soil and nutrient dynamics is largely dependent on the properties of the environment (Muvengwi and others 2013; Van der Plas and others

2013; Davies and others 2014), with higher effects measured in the vertisol than the ferralsol. These findings thus stress the need to consider the interaction between soil properties and termite impacts for a thorough understanding of their effects on ecosystem functioning.

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